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Effect of crowding, food deprivation, and diet on flight initiation and lipid reserves of the lesser grain borer, *Rhyzopertha dominica*

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Abstract

Effects of crowding, food deprivation, and type of cereal diet upon flight initiation, development, body weight, lipid content, and fatty acid composition of the lesser grain borer, *Rhyzopertha dominica* (F.), were studied in two field strains and one laboratory strain. Beetles of all strains reared under crowded conditions had significantly higher flight initiation than beetles reared on isolated kernels (uncrowded). Regardless of degree of crowding, flight initiation increased with the period of food deprivation up to a maximum at 24 h, after which flight initiation declined. Body weight and lipid content decreased as the food deprivation period increased, whereas fatty acid composition was not significantly affected by food deprivation. Beetles from a field strain collected in 1995 had higher flight initiation and increased lipid content compared with beetles from the laboratory strain. However, beetles from the laboratory strain were larger, developed faster, and were more fecund than beetles from this field strain. The cereal diet on which beetles were reared also had a significant effect on flight initiation, lipid content, and fatty acid composition. Beetles reared on whole rice and wheat produced adults with higher flight initiation, higher lipid content, and higher oleic acid concentration than beetles reared on whole corn and sorghum.

Introduction

The lesser grain borer, *Rhyzopertha dominica* (F.) is a specialized grain-feeding member of the family Bostrichidae, a woodboring group of insects (Wright et al., 1990). This species represents one of the major pests of stored grain in the world (Pajni & Shobha, 1979; Barrer et al., 1993; Fields et al., 1993). In the United States, adult insects infest grain soon after it is stored on the farm, generally during the warmest months (Hagstrum & Throne, 1989).

Adult dispersal by flight is a fundamental process in *R. dominica* population dynamics as part of each generation emigrates and colonizes new storage facilities, and this can result in economically important populations within a few weeks of grain storage. Younger adults tend to fly more than older adults (Barrer et al., 1993; Aslam et al., 1994), which indicates that once *R. dominica* infest a bulk of grain, they tend to stay and reproduce rather than leave. For flight to occur, an adequate combination of temperature and light intensity is necessary (Dowdy, 1994). Light intensity affects time of flight, whereas temperature influences the frequency and duration of flight (Lewis & Taylor, 1964). Studies also have shown that depriving recently emerged adults of food for 2 to 3 days results in more flight initiation. However, food deprivation for longer periods of up to 5 days reduces the frequency of flight initiation (Barrer et al., 1993).

Lipids, carbohydrates and, in some insects, certain amino acids are used as respiratory fuels to supply the energy for flight (Beenakkers et al., 1985). Lipids are utilized in migrating insects primarily because they can provide up to eight times more chemical energy than equivalent amounts of carbohydrates (Judge et al., 1991). Lipids accumulated during larval life are the main energy reserve for non-feeding and starved insects (Urs & Hopkins, 1973). The major lipid components in the fat body are triglycerides (Downer, 1985). Fatty acids combined in triglycerides of insect

fats and oils are usually long chain and can be saturated acids, such as palmitic and stearic, or unsaturated acids, such as palmitoleic, oleic, linoleic, and linolenic (Gilby, 1965). However, the fatty acid composition can vary with insect's diet, developmental stage, and environmental conditions (Kuthiala & Chippendale, 1989).

This study compares the rate of flight initiation of insects reared individually to that of insects reared in crowded cultures. It also investigates the correlation of flight initiation with the type of cereal diet on which the insects were reared, food deprivation and their body weight, lipid content and fatty acid composition.

Materials and methods

Culture methods. Insects used in this study were obtained from two field strains and one laboratory strain of *R. dominica* reared on whole kernel, hard red winter wheat at 27 ± 2 °C and 65 ± 5% r.h. The laboratory strain was from the Stored-Product Entomology Laboratory in the Department of Entomology at Kansas State University. This strain has been reared in laboratory conditions for more than 20 years. Two field strains were collected in Manhattan, KS, using Lindgren funnel traps (Lindgren, 1983) baited with wheat and aggregation pheromone (Trece Inc. Salinas, CA). The field strain used in the starvation experiment was collected in July 1995 (Kansas 95), whereas the field strain used in the diet study was collected in September 1996 (Kansas 96). All cultures were maintained in light-tight plywood boxes (25×12.5 cm) with circulating air fans (Aslam et al., 1994). Each box contained 2 Phillips F8T5/CW fluorescent lights (425–470 lux). A L14:D10 photoperiod was used. The boxes were held in a rearing chamber maintained at 27 ± 2 °C and 65 ± 5% r.h.

Flight bioassay. Flight initiation of *R. dominica* was assayed inside the light-tight plywood boxes described above with a flight bioassay developed by Aslam et al. (1994). The assay chamber consisted of a 95-mm-diameter glass funnel with the inner surface coated with sticky material (Sticky Stuff, Olson Products, Medina, OH) and inverted over a petri dish (10×85 mm) containing beetles. The sides of the petri dish were coated with Teflon PTFE 30 fluorocarbon resin (DuPont, Wilmington, DE) to prevent insects from walking onto the funnel edge. Flying beetles were trapped on the sticky inner surface of the funnel.

Effect of crowding on flight initiation. To determine the effect of larval/pupal exposure to crowded or uncrowded rearing conditions on flight initiation of emerging *R. dominica* adults, two rearing methods were used to obtain adult progeny.

Crowded. Adult progeny from crowded cultures were obtained by introducing 350 adults of both sexes on 400 g of whole kernel, hard red winter wheat in quart jars. After 8 days, all introduced adults were removed. Adult progeny (3 to 6 days old) from these cultures were used in flight bioassays.

Uncrowded. Adult progeny from larvae reared in isolated (uncrowded) conditions were obtained as followed. Adults from stock cultures were allowed to lay eggs in 100 g of whole, hard, red winter wheat in quart jars. Eggs were collected every 2 days by sieving. Newly hatched larvae were placed on single kernels of wheat in a multiple-well tissue-culture plate (Corning Laboratory Sciences Co., Corning, NY). Emerging adults (3 to 6 days old) were collected for bioassays.

Flight initiation was assayed with progeny of the 2nd generation of field strains and an unknown generation of the laboratory strain. Eighteen hours prior to the test, batches of 50 unsexed adults 4–6 days old were placed in petri dishes without food, and the dishes were covered with lids. Just before lights were turned on, the petri dish covers were replaced with funnels. The number of adults adhering to the funnels was recorded after 24 h. This flight bioassay was replicated 10 times by using 50 adults of each strain per replicate. The experimental design was a split-plot with rearing method arranged in a 2-by-3 factorial configuration as the main plot and with strain as the subplot level.

Effects of food deprivation. To determine the effects of food deprivation on flight initiation, body weight, lipid content, and fatty acid composition, flight bioassays were carried out with the laboratory and the 1995 field strain. Both strains were reared in crowded and uncrowded conditions.

Adults used in this experiment were deprived of food for 24, 48, and 72 h, and their flight responses were compared with the flight response of unstarved insects. All adults were 5 days old at the time of the flight bioassay. Starved beetles were obtained by placing batches of 50 insects in petri dishes without food. The dishes were covered with lids and placed in the light-tight plywood boxes at 27 ± 2 °C and 65 ± 5% r.h. for 24, 48, or 72 h, after which the petri dish lids were replaced with inverted funnels. Unstarved adults were

placed in groups of 50 in petri dishes with food and 30 minutes later, the petri dish lids were replaced with inverted funnels. The number of beetles adhering to the funnels was recorded after 24 h. The experimental design was a split-plot in a 4-by-2 factorial arrangement, in which food deprivation was tested at four levels and rearing method at two levels. Experiment was replicated 10 times with each strain at each rearing density for a total of 4000 beetles, with 500 tested for each combination of starvation by strain by rearing method.

Three batches of 200 adults, 5 d-old reared in crowded conditions, for each starvation period and each strain were collected from the same generation as adults used in the flight bioassays and used for lipid analysis. The insects were weighed to the nearest 0.1 mg and held at -70 °C until analysis.

Developmental times and fecundities of field and laboratory strains. Preliminary observations showed some differences in developmental times and fecundities between the laboratory and the 1995 field strain used in the previous experiment. To document these strain differences, three parameters were measured: total progeny production, average number of days to egg hatch, and average number of days to adult emergence. Comparisons were made at 27 ± 2 °C, 65 ± 5% r.h. and L14:D10 photoperiod. To compare fecundity, 100 unsexed, two-wk-old adults for both strains were placed in 400 g of hard red winter wheat for oviposition. The wheat was held in quart jars with screen lids. After 7 days, the introduced population was removed and 15 days later, 10 samples of 25 g of infested wheat for each strain were taken from jars. Fifty days later, emerged adults were removed and counted, and the number of adults was recorded.

The average time to egg hatch and to adult emergence was determined. Adults from stock cultures of both strains were allowed to lay eggs in 100 g of hard red winter wheat in quart jars. Eggs were collected every day by sieving and then checked daily for egg hatch. The number of newly hatched larvae was recorded, and each larva was placed on a single kernel of wheat in a multiple-well tissue-culture plates. Forty days later, the infested kernels were checked daily for emerging adults, and the date of eclosion was recorded.

Effects of food source. To assess the effects of different cereal diets on body weight, lipid content, and flight initiation of a field strain of *R. dominica* (1996), cultures were started by placing 350 adults of both sexes on 400 g of whole yellow maize, brown rice, red sorghum, or hard-red winter wheat. Insects were held at 25 ± 2 °C, 65 ± 5% r.h., and L14:D10 photoperiod. Flight bioassays were carried out with the second generation of beetles reared from each cereal. Eighteen hours before the flight assay, 10 groups of 50 unsexed adults, 4 to 6 days old, were selected from each cereal and placed without food in petri dishes. Each treatment was replicated 10 times for a total of 500 beetles per cereal. The number of beetles that flew was recorded after 24 h. The experiment was conducted in a 4-by-2 factorial arrangement, and data were analyzed using a split-plot design, with diet as main plot and rearing method as subplot.

Three batches of 200 adults, 5 d-old were collected for lipid analysis for each food source from the same generation as adults used in the flight bioassays. The adults were weighed and held at -70 °C until analysis.

Lipid extraction and analysis of whole insects. Batches of 200 adults collected from the food deprivation and food source experiments were placed in glass vials containing liquid nitrogen and ground to a fine powder with a glass rod. The liquid nitrogen was allowed to evaporate, and chloroform (10 ml) was added to each sample and left to stand for 1 h to extract the lipids. The chloroform extract was filtered through two thicknesses of Whatman No. 1 filter paper and evaporated to dryness under a stream of nitrogen in a preweighed vial. After the lipid weight was determined, the sample was dissolved in chloroform. Samples containing at least 2 mg lipid were used for fatty acid analysis.

Fatty acid determination. The fatty acid composition of lipid samples was determined as follows. The chloroform added to the 2 mg lipid samples was evaporated under nitrogen, and the samples were placed in reaction vials containing 200 μl of 0.5 M NaOH in methanol that were capped and heated at 100 °C for 1 h. After cooling, 200 μl of BF_3 (14%) in methanol was added to each vial. These vials were capped and heated at 100 °C for 2 min. After cooling, the contents of these vials were partitioned against hexane. The hexane layer containing the fatty acid methyl esters was collected, and 2 μl injected into a Tracor 540 gas chromatograph equipped with a capillary column (SGE BP1, equivalent to OV101 SE30, 0.33 mm ID $\times$ 25 m) and a flame ionization detector. Nitrogen carrier gas had a head pressure of 6 psi, and the col-

umn oven was temperature programmed from 150 °C (1 min hold) to 300 °C (5 min hold) at 3.5 °C/min. The temperature of the injector and detector was 325 °C.

Fatty acid methyl ester standards of lauric acid, myristic acid, palmitic acid, stearic acid, oleic acid, and linoleic acid also were prepared as above. Retention times and relative areas of each fatty acid were recorded with a Shimadzu integrator (Kyoto, Japan) and compared with those of standards. Percentage composition of each fatty acid in the lipid extract of each treatment was calculated.

Statistical analysis. Mean values, mean separation, and analysis of variance (ANOVA) were determined with SAS Procedures ANOVA, GLM, and REG (SAS Institute, 1985). Mean separations were done by using least significant differences (LSD) in SAS (Steel & Torrie, 1980).

Results

Effect of crowding on flight initiation. Flight initiation among strains of *R. dominica* was significantly affected by strain ($F = 101.7$; $df = 2, 54$; $P < 0.01$) and rearing conditions ($F = 88.7$; $df = 1, 54$; $P < 0.01$). The interaction for strain-by-rearing method also was highly significant ($F = 5.2$; $df = 2, 54$; $P < 0.01$). Therefore, we analyzed the data by rearing condition. Significantly more beetles from crowded rearing conditions initiated flight compared to those from uncrowded cultures with the Kansas 95 ($F = 59.7$, $df = 1, 18$, $P < 0.01$), Laboratory ($F = 75.2$, $df = 1, 18$, $P = 0.01$) and Kansas 96 ($F = 20.3$, $df = 1, 18$, $P < 0.01$) strains (Figure 1). Significantly more beetles from the field strain collected in Manhattan, KS in 1995 initiated flight compared to beetles from the laboratory strain in both crowded ($F = 55.6$; $df = 2, 27$; $P < 0.01$) and uncrowded cultures ($F = 48.8$; $df = 2, 27$; $P < 0.01$) (Figure 1).

Effect of food deprivation on flight propensity. The strain-by-starvation period interaction was significant ($F = 9.8$; $df = 3, 79$; $P < 0.01$) and therefore the effects of starvation period were analyzed separately for each strain. For the 1995 field strain, flight initiation varied significantly with starvation period for insects from crowded ($F = 13.8$, $df = 3, 36$, $P < 0.01$) and uncrowded ($F = 18.2$, $df = 3, 35$, $P < 0.01$) cultures (Figure 2). For the laboratory strain, flight initiation also varied significantly with starvation period for insects from crowded ($F = 17.9$, $df = 3, 36$, $P < 0.01$) and uncrowded ($F = 2.9$, $df = 3, 36$, $P < 0.05$) cultures. Rearing density significantly influenced flight initiation with all starvation periods, strains, and densities ($F > 31.6$, $df = 1, 18$, $P < 0.01$).

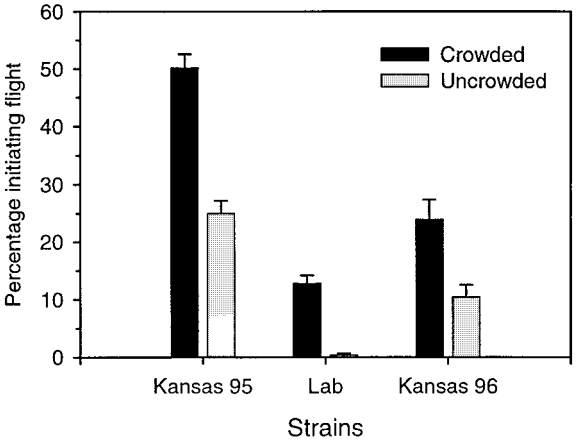

Figure 1. Effect of crowding on flight initiation of three strains of the lesser grain borer, *Rhyzopertha dominica* (F.). Percentage of insects initiating flight (Mean ± SEM) from 10 replicates per strain, 50 insects per replicate.

Effect of food deprivation on body weight and lipid content. Fresh body weight, total lipid content, and percentage of lipids decreased in both strains of *R. dominica* as the period of food deprivation period increased (Figure 3). Unstarved insects and those deprived of food for 24 h reared in crowded conditions were heavier (Figure 3A), had more total lipids (Figure 3B), and had higher percentage lipid (Figure 3C) based on fresh body weight than insects deprived of food for 48 and 72 h. The adults from the laboratory strain were significantly heavier than adults from the 1995 field strain ($F = 31.2$; $df = 7, 16$; $P < 0.01$). However, the total lipid content ($F = 31.3$; $df = 7, 16$; $P < 0.01$) and the percentage of lipid (Figure 3B) ($F = 37.8$; $df = 7, 16$; $P < 0.01$) were significantly higher in the body of adults from the 1995 field strain compared to those from the laboratory strain. Total lipid decreased as starvation period increased. This relationship was described by the following equations:

$$Y = 109.7(\pm 4.72) - 0.892(\pm 0.105)x \quad \text{for}$$

field strain ($r^2 = 0.88$; $n = 12$; $P < 0.01$),

$$Y = 79.4(\pm 2.93) - 0.506(\pm 0.0652)x \quad \text{for}$$

laboratory strain ($r^2 = 0.86$; $n = 12$; $P < 0.01$)

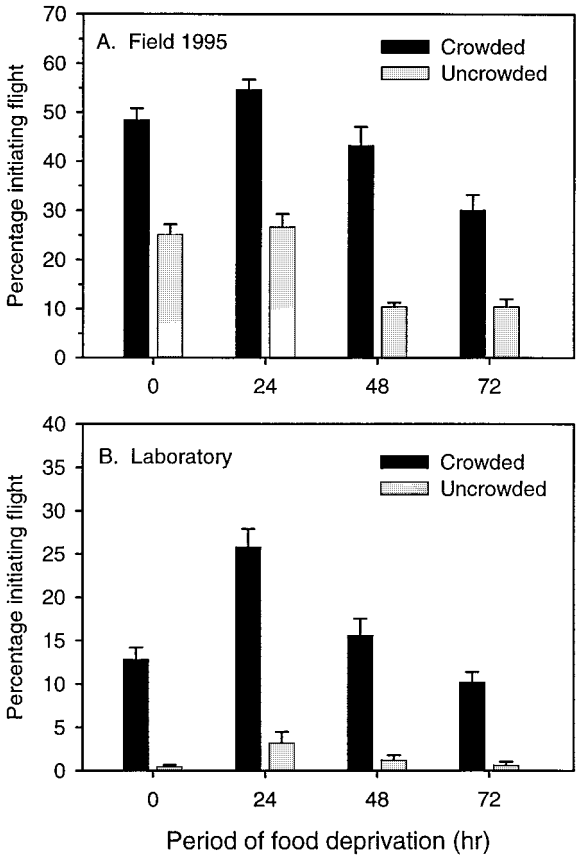

Figure 2. Effect of food deprivation on flight initiation of two strains of the lesser grain borer, *Rhyzopertha dominica* (F.). Percentage of insects initiating flight (Mean ± SEM) from 10 replicates per food deprivation period, 50 insects per replicate.

where Y = amount of lipid (μg/insect) and x = starvation period (hours).

Effect of food deprivation on fatty acid composition. The most abundant fatty acid found in both strains and in the four periods of starvation was oleic acid, followed by palmitic, linoleic, stearic, palmitoleic, and myristic (Table 1). Although no significant difference was found ($F = 1.4$; $df = 7, 16$; $P < 0.23$), palmitic acid tended to decrease as food deprivation increased in both strains (Table 1).

Effect of strain on developmental and reproductive parameters. Hatching time was significantly shorter for eggs laid by females from the laboratory strain than for eggs laid by females from the 1995 field strain ($F = 40.9$; $df = 1, 198$; $P < 0.01$) (Table 2). The average number of days from egg hatch to adult emergence also was significantly shorter for the laboratory strain

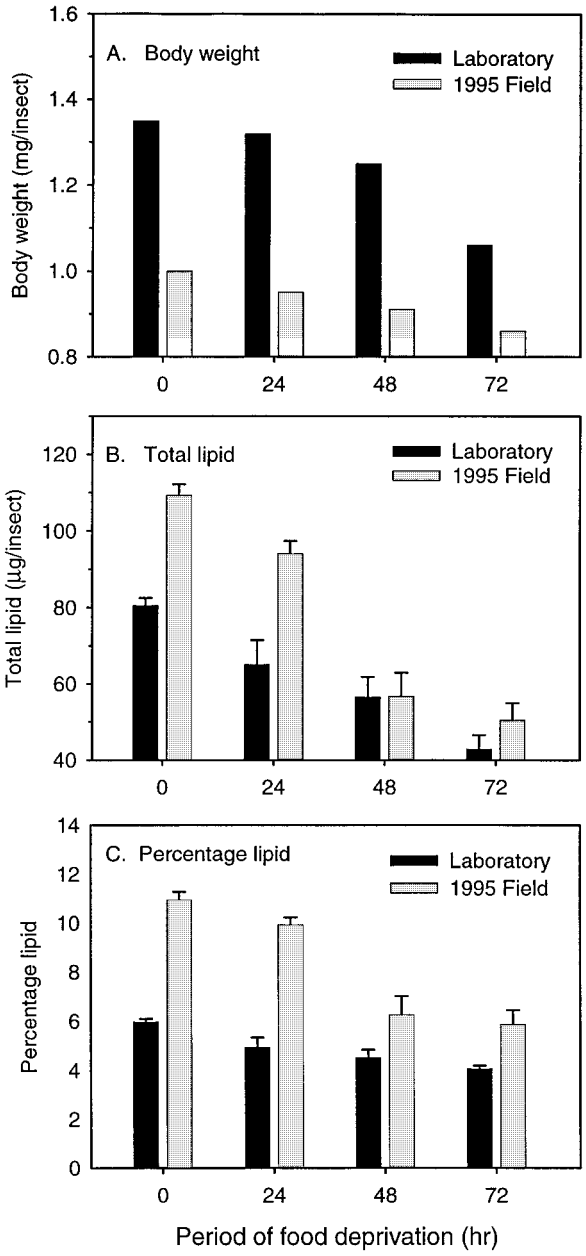

Figure 3. Effect of food deprivation on body weight, total lipid, and percentage lipid content per unit of body weight of two strains of lesser grain borer, *Rhyzopertha dominica* (F.) reared in crowded conditions. Mean ± SEM of 3 replicates per treatment, 200 insects per replicate.

Table 1. Percentage composition of fatty acids (mean ± SEM) in the total lipid fraction of whole body extracts of two strains of *Rhyzopertha dominica* reared in crowded conditions and exposed to different periods of food deprivation[a]

	Starvation period			
Fatty acids	0 h	24 h	48 h	96 h
Laboratory strain				
Myristic (C14)	0.4 ± 0.01	0.4 ± 0.01	0.4 ± 0.01	0.3 ± 0.01
Palmitic (C16)	31.2 ± 0.52	29.7 ± 0.92	28.2 ± 1.04	27.5 ± 1.13
Palmitoleic (C16:1)	0.6 ± 0.02	0.6 ± 0.02	0.6 ± 0.02	0.6 ± 0.02
Stearic (C18)	4.3 ± 0.13	4.5 ± 0.14	4.8 ± 0.23	5.0 ± 0.21
Oleic (C18:1)	43.6 ± 0.94	43.3 ± 0.82	43.8 ± 1.12	44.6 ± 1.13
Linoleic (C18:2)	21.9 ± 0.63	22.0 ± 0.71	21.7 ± 0.92	21.4 ± 0.84
1995 field strain				
Myristic (C14)	0.3 ± 0.01	0.3 ± 0.01	0.3 ± 0.01	0.3 ± 0.01
Palmitic (C16)	28.1 ± 1.43	27.3 ± 1.22	26.7 ± 1.21	25.3 ± 1.32
Palmitoleic (C16:1)	0.6 ± 0.02	0.6 ± 0.02	0.6 ± 0.02	0.6 ± 0.02
Stearic (C18)	4.0 ± 0.44	3.8 ± 0.51	3.9 ± 0.42	3.9 ± 0.43
Oleic (C18:1)	43.5 ± 1.51	43.7 ± 1.43	43.3 ± 1.24	43.2 ± 1.41
Linoleic (C18:2)	24.1 ± 0.43	24.3 ± 0.42	24.0 ± 0.54	24.3 ± 0.54

[a]No significant differences occurred among the levels of fatty acids during the periods of starvation.

than for the 1995 field strain ($F = 36.5$; $df = 1, 184$; $P < 0.01$). Finally, total progeny production was significantly greater in the laboratory strain than in the Kansas 95 strain ($F = 58.5$; $df = 1, 18$; $P < 0.01$) (Table 2).

Effect of food source on flight initiation. Flight initiation was significantly affected by food source ($F = 46.2$; $df = 2, 54$; $P < 0.01$), and rearing method ($F = 11.2$; $df = 1, 54$; $P < 0.01$). Because the interaction between food source and rearing method was highly significant ($F = 3.8$; $df = 2, 54$; $P < 0.02$), we analyzed the rate of flight initiation by rearing method. The mean number of beetles that initiated flight was significantly greater among progeny of insects reared in rice or wheat than for those reared in sorghum or corn (Figure 4) in both crowded ($F = 33.2$; $df = 3, 36$; $P < 0.01$) and uncrowded rearing conditions ($F = 39.6$; $df = 2, 27$; $P < 0.01$). Because corn was the poorest food source for this species, we were unable to rear insects on individual corn kernels.

Effect of food source on body weight and lipid content. Body weight of beetles reared in the four cereals was not significantly different ($F = 3.3$; $df = 3, 36$; $P < 0.23$) (Table 3). Total lipid content of the beetles reared in rice was significantly greater than that of beetles reared in wheat, corn, or sorghum ($F = 17$; $df = 3, 8$; $P < 0.01$) (Table 3). Percentage of lipid based on fresh body weight also was significantly higher in adults reared in rice ($F = 22.4$; $df = 3, 8$; $P < 0.01$). Beetles reared in rice and wheat had 2.2-fold and 1.6-fold, respectively, more lipids as a percentage of fresh body weight than those beetles reared in sorghum and corn (Table 3).

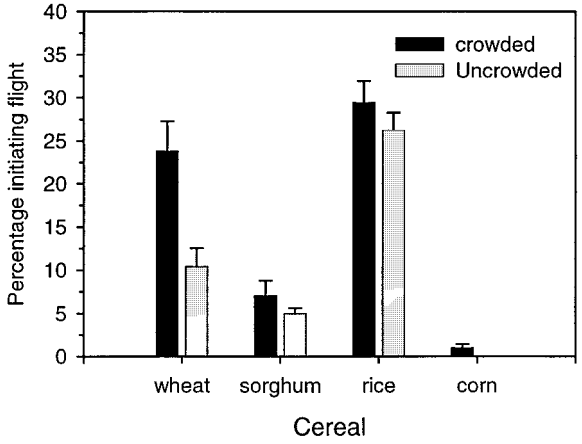

Figure 4. Flight initiation of a 1996 field strain of the lesser grain borer, *Rhyzopertha dominica* (F.) reared for two generations on different types of cereal. Percentage of insects initiating flight (Mean ± SEM) from 10 replicates per type of cereal, 50 insects per replicate.

Table 2. Egg hatch time, adult emergence time, and total progeny production (mean ± SEM) of unsexed adults during a 7-day oviposition period for one laboratory strain and one field strain collected in Manhattan, KS in 1995 of *Rhyzopertha dominica* reared in crowded conditions at 25 ± 2 °C and 65 ± 5% r.h.

Strain	Egg hatch time (days) Ψ	Adult emergence time (days) Φ	Total progeny[a]
Laboratory	8.2 ± 0.1a	42.9 ± 0.1a	170.5 ± 16.8a
Kansas 95	8.9 ± 0.1b	44.6 ± 0.2b	40.8 ± 1.9b

Means in a column followed by different letters are significantly different ($P < 0.01$).
Ψ Average number of days from egg hatch (based on 100 eggs).
Φ Average number of days from egg to adult emergence (based on 100 individuals).
[a]Mean total progeny from 100 adults/1000 g of wheat.

Table 3. Body weight, total lipid content, and percentage of lipid (mean ± SEM) in whole insects from the second generation of *Rhyzopertha dominica* reared in crowded conditions on four types of grain

Types of cereal	Fresh body weight (mg/insect)[a]	Total lipid content (μg/insect)[a]	% lipid/fresh body weight[a]
Rice	1.0 ± 0.0a	129.5 ± 10.3a	13.0 ± 1.0a
Wheat	1.0 ± 0.0a	93.0 ± 10.5b	9.2 ± 0.8b
Sorghum	1.0 ± 0.0a	59.7 ± 2.8c	6.0 ± 0.3c
Corn	0.98 ± 0.0a	64.3 ± 2.4c	6.6 ± 0.2c

[a]Means in a column followed by different letter are significantly different ($P < 0.01$).

Effect of food source on fatty acid composition. Oleic, palmitic, and linoleic acids constituted more than 95% of the total fatty acids in lipid extracts of whole insects from the populations of *R. dominica* reared in 4 different grains (Table 4). The percentage of oleic acid (the predominant fatty acid) was significantly higher in beetles reared in rice ($F = 344.4$; $df = 3, 8$; $P < 0.01$). Palmitic acid was significantly higher in beetles reared in wheat ($F = 97.1$; $df = 3, 8$; $P < 0.01$), whereas linoleic acid was significantly higher in insects reared in corn ($F = 424.9$; $df = 3, 8$; $P < 0.01$). Stearic, palmitoleic, and myristic acids represented less than 5% of the total fatty acids found and did not vary significantly among the populations on the 4 grains tested.

Discussion

Crowding had a dramatic effect on flight initiation in both laboratory and field strains of *R. dominica* in this study. Barrer et al. (1993) also showed that *R. dominica* reared at high density tended to initiate flight significantly more than insects reared at lower densities. Similarly, Fadamiro et al. (1996) found that *Prostephanus truncatus* (Horn) reared at a density of 500 adults in 250 g of whole maize initiated flight significantly more than those beetles reared at a lower density of 5 adults per 250 g. Observed higher amounts of frass (waste material) and damaged kernels under crowded conditions in our experiments suggest that increased flight tendencies are an adaptation to avoid inadequate food resources and inferior food quality for succeeding generations. For example, poor resource quality in crowded populations and its contribution to flight initiation of *R. dominica* and *P. truncatus* also were noted by Barrer et al. (1993) and Fadamiro et al. (1996).

In the current study, significantly more progeny from both field strains of *R. dominica* had initiated flight compared to progeny from the laboratory strain. This tendency was also noted by Aslam et al. (1994). This suggests that as populations become adapted to laboratory conditions, the need to fly to find new food sources is reduced, and their flight behavior is subsequently altered.

Food deprivation had a similar effect on field and laboratory strains of *R. dominica* that were tested. Numbers of beetles initiating flight reached a maximum after 24 h of starvation and declined significantly with longer periods of food deprivation. This pattern was more evident in the laboratory strain of beetles

Table 4. Percentage composition of fatty acids (mean ± SEM) in the total lipid fraction of whole body extracts from the F2 generation of *Rhyzopertha dominica* reared in crowded conditions on four types of grain[a]

Fatty acids	Types of cereal			
	Rice	Wheat	Sorghum	Corn
Myristic (C14)	0.4 ± 0.01a	0.5 ± 0.02a	0.3 ± 0.02a	0.3 ± 0.02a
Palmitic (C16)	30.6 ± 0.3bc	35.3 ± 0.24a	30.0 ± 0.21c	31.4 ± 0.01b
Palmitoleic (C16:1)	0.6 ± 0.01a	0.7 ± 0.03a	0.7 ± 0.10a	0.7 ± 0.22a
Stearic (C18)	3.7 ± 0.07a	3.4 ± 0.09a	3.3 ± 0.12a	3.7 ± 0.20a
Oleic (C18:1)	59.8 ± 0.20a	45.8 ± 0.43b	44.2 ± 0.31c	41.0 ± 0.31d
Linoleic (C18:2)	4.3 ± 0.21d	14.1 ± 0.07c	21.9 ± 0.40b	23.5 ± 0.20a

[a]Means within a row with different letters are significantly different ($P < 0.01$).

reared in both crowded and uncrowded conditions. These results suggest that young adults of *R. dominica* respond to short periods of starvation by initiating flight. The effect of food deprivation on flight initiation of *R. dominica* also was noted by Barrer et al. (1993), who pointed out that starvation for 4 to 5 days tended to reduce the number of beetles that initiated flight. In contrast with our results, Barrer et al. (1993) found that newly emerged adults starved for 48 or 72 h tended to show greater flight initiation. Fadamiro & Wyatt (1995) reported that flight initiation of *Prostephanus truncatus* increased with starvation periods up to a maximum at 48 h and then declined.

A significant loss of fresh body weight and lipid occurred in beetles from both strains when they were deprived of food for more than 48 h. A 50% loss in lipids occurred after 72 h of starvation in both strains. Although beetles deprived of food for 24 h had enough energy reserves to fly, both flight initiation and lipid decreased rapidly as starvation period increased. Although direct evidence that *R. dominica* uses lipid for flight is not yet reported, our results suggest that the low flight initiation of beetles deprived of food for more than 48 h occurred as a result of lower available energy resources. The importance of lipids as fuel for flight is well known (Beenakkers et al., 1985). Food deprivation reduced carbohydrate and lipid levels in cockroaches by depletion of available reserves (Downer, 1985).

Although beetles from the laboratory strain were heavier than beetles from the field strain, the total percent lipid content was higher in beetles from the field strain, which showed high flight initiation. This suggests that field strains, which disperse to find new food sources, need to have larger energy reserves for flight, whereas beetles from the laboratory strain (weak fliers) allocate most of their lipid reserves to reproduction. This is supported further by our results from the developmental parameters between the two strains. Egg hatch and adult emergence were significantly earlier, and progeny production was significantly greater in the laboratory strain compared with the field strain. This suggests that an inverse relation may exist between flight and reproductive potential of the strains tested. However, more detailed studies are necessary to confirm whether or not there is a trade-off between flight and reproduction in *R. dominica*.

Percentage composition of fatty acids of the unstarved and starved insects varied only slightly in both strains, indicating that the decrease in total lipids in the starved insects was not accompanied by changes in the ratios of fatty acids utilized during starvation. Only a small tendency for decreasing concentration of palmitic acid occurred as the insects were starved. Nwanze et al. (1976) and Urs & Hopkins (1973) also reported similar concentrations of fatty acids in the fat body of cowpea weevils, *Callosobruchus maculatus*, and *Tenebrio molitor*, respectively.

Flight initiation of *R. dominica* also was affected strongly by the diet upon which the beetles were reared. More beetles reared in rice and wheat initiated flight than beetles reared in corn and sorghum in both crowded and uncrowded rearing conditions. Although progeny were not counted, we observed noticeably more adult progeny in rice and wheat cultures than in corn and sorghum cultures. These data provide some basis for previous observations that *R. dominica* is found most commonly in stored rice and wheat in storage facilities around the world (Cogburn et al., 1984; Pedersen, 1992; Hagstrum & Flinn, 1994).

Corn and sorghum provided much less favorable substrates for development of *R. dominica* than wheat

and rice. Although adult body weights of beetles reared in the four types of grain were similar, the percentages of lipid for each population varied significantly. Beetles reared in rice and wheat contained 2.2-fold and 1.6-fold more lipids than those beetles reared in corn and sorghum, respectively. These results may partially explain the differences in flight activity among the four populations. The same tendency also was reported with *Ips calligraphus* reared in slash pine bolts with thick or thin phloem (Slansky Jr. & Haack, 1986); insects reared in thick phloem produced individuals with greater lipid reserves and greater capacity for flight.

Diet also exerted a significant effect on fatty acid composition of the total lipid fraction from beetles reared in the four types of grain. Relative amounts of the major fatty acids present varied in the four populations. Beetles reared on rice had the highest concentration of oleic and the lowest concentration of linoleic acids, whereas insects reared on corn had the highest concentration of linoleic and the lowest concentration of oleic acids. Changes in fatty acid composition influenced by the diet on which insects were reared also were noted by Stanley-Samuelson et al. (1988) and Kuthiala and Chippendale (1989).

This research has offered some insight into flight behavior of *R. dominica* under different circumstances. Beetles reared under crowded conditions were more likely to fly than those reared under uncrowded conditions, and short periods of food deprivation increased the likelihood of flight. Beetles reared on rice and wheat flew more often than those reared on corn and sorghum. A better understanding of the factors influencing insect flight should help us to improve insect pest management programs for stored wheat.

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